Damage Potential of Grasshoppers (Orthoptera: Acrididae) on Early Growth Stages of Small-Grains and Canola Under Subarctic Conditions

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J. Econ. Entomol. 96(4): 1193-1200 (2003)

ABSTRACT We characterized the type and extent of grasshopper injury to above- and belowground plant parts for four crops [barley (Hordeum vulgare L.), oats (Avena sativa L.), wheat (Triticum aestivum L.), and canola (Brassica campestris L.)] commonly grown, or with potential to grow, in central Alaska. Cages were placed on 48 pots containing plants in second to third leaf stages and stocked with 0, 2, 4, and 6 first-instar *Melanoplus sanguinipes* \overline{F} . pot⁻¹. Plants were harvested $2\overline{2}$ d after planting. Stem growth of barley and oats was not affected except at the highest grasshopper treatment. In canola, stem biomass was reduced at the medium and high grasshopper treatments, when most of the leaves had been consumed. The highest grasshopper treatment reduced leaf area in barley and oats by \approx 55%, and caused a significant reduction in dry weight of leaves, stems, and roots (41–72%). Wheat and canola plants were smaller than barley and oats across all treatments and, at the highest grasshopper density, above-ground portions of wheat and canola were completely destroyed. Length and surface area of roots of barley and oats were reduced by 20–28% again at the highest grasshopper density, whereas the reduction for wheat and canola ranged from 50 to 90%. There was little or no difference among all grasshopper densities for C-N ratio in leaf and stem tissues of all crops. The results suggest that wheat and canola are more susceptible than barley and oats and that densities ≥ 2 pot⁻¹ $(\approx \geq 50 \, \mathrm{m}^{-2})$ of even very small grasshoppers could cause significant damage in small-grain and oilseed crop production.

KEY WORDS *Melanoplus sanguinipes*, small-grains, oilseed crop, grasshopper density, above- and below-ground growth

Many species of grasshopper are well adapted to the habitats created by western agricultural practices (Pfadt 1994). Since the inception of agriculture, grasshoppers have been one of the most important pests of agriculture in almost every part of the world (Gangwere et al. 1997, Weiland et al. 2002). During outbreaks, grasshoppers can cause widespread and severe damage to grasslands, forage, cereal, vegetable, and orchard crops (Wright 1986, Pfadt 1994, Olfert and Slinkard 1999, Lockwood et al. 2002). Over the past 50 yr, grasshoppers were estimated to have caused an average annual crop loss of \$6 million to cereal crops, with losses as high as \$200 million in an outbreak year in Canada and the United States (Gage and Mukerji 1978, Olfert 1986).

One of the most serious grasshopper pest species in North America is the migratory grasshopper, *Melanoplus sanguinipes* F, which is responsible for more damage in crops and grasslands in the United States than any of the other grasshopper species (Pfadt 1994, Otte 1995). The migratory grasshopper has a very wide geographic range, from the tropical lowlands of Mexico (Hebard 1929, Shotwell 1941, Alexander 1941, Vickery and Kevan 1983, Otte 1995) to central Alaska. In Alaska, during outbreaks in 1988, 1992, and 1994,

grasshoppers, primarily *M. sanguinipes* but also *M. borealis* (Fieber) and *Camnula pellucida* (Scudder), inflicted heavy losses on cereal crops and vegetables (Donald et al. 2002).

Yield losses from grasshoppers depend on many factors including grasshopper density, growth stage, their size, weather conditions, and plant vigor. Several studies in temperate and tropical regions have been conducted to determine the relationship between grasshopper density, damage, plant growth, and yield loss in crops and rangelands (Pickford and Mukerji 1974, Capinera and Roltsch 1980, Wright 1986, Olfert and Slinkard 1999). Most of these studies have only measured the yield loss without any examination of plant growth response to grasshopper feeding injury. Unless the plant growth response is understood, it is difficult to develop robust models of insect damage/ yield loss relationships. Morphological and physiological responses of plants to insect feeding damage include changes in growth and allocation of resources to different parts of the plant (Buntin 1991, Hinks and Olfert 1992, Meyer 1998, Olfert and Slinkard 1999).

Crop damage can occur early in the growing season when newly hatched grasshoppers invade the crop from heavily infested areas (such as stubble or road-

side), or when crops are seeded in infested stubble (Pickford and Mukerji 1974, Pfadt 1994, Milbrath et al. 1998). Grain yield depends on the initial development and growth of seedlings, especially in the subarctic where the growing season is short and time is critical for seedling establishment. Photosynthesis and allocation of photosynthate among leaves, stems, and roots are critical in seedling establishment of many crops. Most attention has focused on the effects of grasshopper feeding on above-ground plant biomass, whereas few studies have investigated the effect on below-ground plant biomass. In the past, root weight and length have been used most often to evaluate root systems (Tennant 1975, Murphy and Smucker 1995), largely because of the unavailability of techniques to measure other variables of root morphology, such as surface area, diameter, and branching patterns. Any damage that occurs on the above-ground plant parts may ultimately change the root system and subsequent nutrient-water uptake, thus slowing recovery from the damage and reducing final yield.

The objective of this study was to quantify and characterize the effect of grasshopper feeding on the early growth and morphology (above- and below-ground) of four crops (barley, oats, wheat, and canola) under subarctic conditions. Although barley and oats are the commonly grown crops in Alaska, wheat and canola are being considered as potential crops. Thus, we found it appropriate to include wheat and canola in the experiment. To test the hypothesis that the carbon to nitrogen ratio would be less affected by chewing insects like grasshoppers that remove whole plant parts, the allocation of carbon and nitrogen to leaves and stems was also examined.

Materials and Methods

The damage caused by grasshoppers on early growth of small-grain and oilseed crops was studied within a controlled environment chamber at the University of Alaska Fairbanks. Seeds of each crop were seeded directly into plastic growing pots (0.2 m diameter × 0.4 m depth) filled with sand. Sand was chosen as a growing medium because it makes the study of root morphology and architecture easier. To provide plants with adequate nutrients, we used a controlled release fertilizer (Osmocote, Hummert Int., Earth City, MO). Each pot received 2.5 g of 15-9-12 N-P-K (nitrogen-phosphorus-potassium). One to 2 d after emergence, seedlings were thinned to eight per pot for the small grains (barley 'Otal', oats 'Toral', and wheat 'Ingal') and four seedlings per pot for canola ('Colt'), densities equivalent to field populations. Plants were watered 2-3 times a week.

A split-plot design with three replications was used in the experiment. Crop and grasshopper density were arranged randomly as the main and subplot treatments, respectively. There were four levels of grasshopper density: 0, 2, 4, and 6 pot⁻¹ (approximately equivalent to 0, 50, 100, and 150 hoppers m⁻²) densities that span values found in the field. There were a total of 48 cages. Cages were stocked with first instars

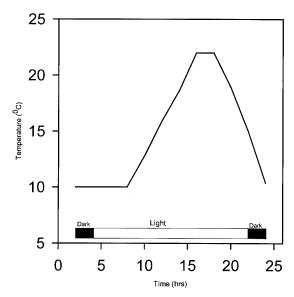


Fig. 1. Diurnal cycle of photoperiod and temperature in a controlled-environment chamber.

of a nondiapausing strain of *M. sanguinipes* when plants were at the second to third leaf stages (method of Haun, 1973), 8–10 d postplanting. This approximates the coincident phenologies of crops and grasshoppers in central Alaska. Grasshoppers in cages were checked almost daily, and dead grasshoppers were replaced to maintain the desired grasshoppers densities.

Temperature and photoperiod conditions of the chamber approximated interior Alaska field conditions (Fig. 1). Relative humidity was around 50%, and temperatures approximated mean daily highs and lows in June in interior Alaska (Fig. 1). The internal body temperatures of the grasshoppers were likely to be higher than ambient temperatures during the photophase because they were able to thermoregulate by climbing to the top of the cages (≈50 cm from the lights) and absorb thermal radiation from the incandescent lamps. Cool-white, very high output (VHO) fluorescent lamps and 100 watt incandescent lamps provided 250-350 µmol m-2 s-1 photosynthetic photon flux (PPF) at the top of the canopy inside the cages, as measured with a PAR-meter (Basic quantum meter, Spectrum Technologies, Inc., Plainfield, IL). Photoperiod was ≈20 h (Fig. 1), which provided enough light for plant growth. During clear days in interior Alaska (latitude 64 ° N) near the summer solstice, sunlight provides a mean daily PPF of ≈500 μmol m-2 s-1 (Bonanza Creek LTER 2001). Even though the instantaneous PPF levels were lower than the mid-day PPF peak levels in the field, the dailyintegrated PPF levels are typical of field values in interior Alaska. Partly cloudy days are very typical of the early summer weather patterns in interior Alaska. Further, Chabot et al. (1979) showed that leaf anatomy and photosynthesis are more influenced by the daily-integrated PPF than the instantaneous PPF.

Table 1. Analysis of variance showing probabilities and F values for the main and interaction effects on the above-, below-ground dry matter, and carbon to nitrogen ratio of plant parts

	df							Ca	Carbon to nitrogen ratio		
Source		Dry weight				Root Morphology		Crop group 1 ^a		Crop Group 2	
		Leaf area	Leaf	Stem	Root	Length	Diameter	Leaf	Stem	Leaf	Stem
		$\phantom{aaaaaaaaaaaaaaaaaaaaaaaaaaaaaaaaaaa$									
Crop (C)	$3,1,1^{b}$	<0.0001 200.41	<0.0001 427.26	<0.0001 488.08	<0.0001 194.62	<0.0001 475.92	<0.0001 135.22	0.2044 3.45	0.1890 3.84	0.1103 7.59	0.2106 3.31
Error block \times C	6,2,2										
Grasshopper	3,3,2	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.2544	0.0381	0.0547	0.9845	0.8920
Density (GD)		63.39	98.10	30.45	46.24	26.85	1.45	3.86	3.37	0.02	0.12
$C \times GD$	9,3,2	0.1182 1.81	0.0031 4.01	0.3259 1.23	0.0197 2.85	0.9373 0.37	0.5449 0.89	0.5019 0.83	0.5714 0.70	0.8913 0.12	0.9429 0.06
Error	47,23,17										

^a Crop grouping 1, barley and oats; crop grouping 2, wheat and canola.

Plants were harvested 22 d after planting. In each treatment, plants were separated into leaves, stems and roots. Leaf area (cm²) was measured with a Li-Cor 3000 model leaf area meter. Plant material was dried for 24 h at ≈70°C and dry weight of each fraction was determined. Measurements were expressed on a per pot basis. The leaf and stem parts were ground and ≈200 mg of each sample was analyzed with a LECO 2000 CHNS analyzer for dry combustion determination of total C and N concentration in the leaf and stem part of the plants. In the case of wheat and canola. there was not enough stem or leaf tissue remaining in the highest grasshopper density treatment for analysis. As a result, crops for this particular variable were grouped as group 1 (barley and oats) with four levels of grasshopper densities and group 2 (wheat and canola) with three levels of grasshopper densities and analyzed separately. Therefore comparisons of the crops for CN data were made within each group (Table 1).

Roots were gently separated from the growing media by immersing the whole pot in water and gently loosening the sand and roots together out of the pots. Once the whole root mass was out of the pot \approx 80% of

the root system could be collected simply by floating them in a large quantity of water. A 0.3-mm diameter sieve was used to separate the remaining roots from the sand and water. Some of the organic debris was removed by hand and this was done during repeated gentle washing using a much smaller plastic container filled with water. Because root image analyses were not done right away, roots were kept fully immersed in a 20% aqueous ethanol solution.

Root image analysis (for total root length, root surface area, average root diameter, and root volume) were done with interactive, scanner-based image analysis software that controlled scanning, digitizing, and analysis of root samples (WinRHIZO version (5.0); Regent Instruments, Quebec, Canada). Roots were scanned on a Hewlett-Packard scanner, at 118 dots per cm (300 dots per inch) scanning resolution. The scanner incorporated two light sources, one under the cover of the scanner and the other below as part of the scanner main body, to eliminate shadows that could confuse the analysis. The whole root system of each treatment was divided into eight (for small grains) and four (for the canola) approximately equal parts and put in a Petri dish filled with toluidine blue stain (0.1%

Table 2. Values of variables expressed as a percentage of controls

Crop	Grasshoppers	Leaf area		Dry weight	Root		
	per pot		Leaf	Stem	Root	Length	Diameter
Barley	0						
Barley	2	79.53	77.42	96.84	87.30	88.43	98.36
Barley	4	63.85	67.05	89.36	69.25	81.27	99.52
Barley	6	43.15	42.04	59.19	57.76	73.92	105.29
Oats	0						
Oats	2	66.10	74.43	92.26	89.86	87.70	98.09
Oats	4	49.06	62.69	79.81	68.24	80.00	98.61
Oats	6	46.06	43.84	60.39	57.24	72.39	93.79
Wheat	0						
Wheat	2	13.16	15.13	40.31	68.67	70.02	97.53
Wheat	4	11.67	12.73	31.91	40.18	56.72	92.07
Wheat	6	0.00	0.00	0.00	24.72	46.41	104.29
Canola	0						
Canola	2	55.84	80.14	93.65	61.70	35.12	96.89
Canola	4	26.63	37.93	34.32	54.83	22.30	88.19
Canola	6	0.00	0.00	0.00	27.95	9.81	97.43

^b Values of degree of freedom are for above- and below-ground, crop group 1 and crop group 2 variables, respectively.

wt:vol) for $\approx\!10$ min. After immersion, excess stain was removed from the roots by rinsing them under running tap water for $\approx\!1$ min (Costa et al. 2000). Root samples were placed in the Plexiglas trays (20 \times 30 cm) with a 0.3–0.4-cm deep layer of distilled water. The water was used to untangle the roots as much as possible to minimize root overlapping and crossing over (Costa et al. 2000). The average of eight and four values for smallgrains and canola, respectively, were used for treatment comparisons.

The experiment was repeated. Because variances and means of the experiments were homogenous, data of the two experiments were pooled (Steel and Torrie 1980). The statistical analyses were performed using the GLM procedure of SAS (SAS Institute 1994) for all analyses, $\alpha=0.05$. Additionally, multiple pair-wise comparisons were performed using least significant difference (LSD) (P<0.05) tests.

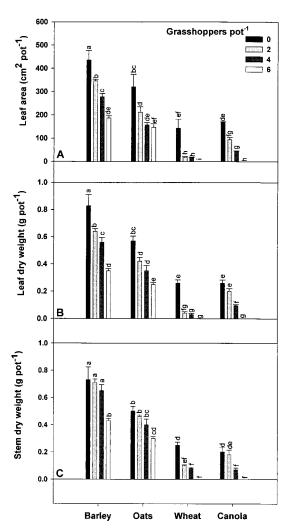


Fig. 2. Effects of grasshopper feeding on dry matter and leaf area of four crops. (A, leaf area; B, leaf dry weight; C, stem dry weight). Bars with the same letter are not significantly different according to Fisher LSD test (P < 0.05).

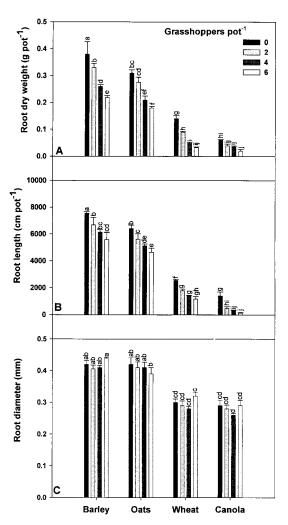


Fig. 3. Effects of grasshopper feeding on root growth of four crops. (A, root dry weight; B, total root length; C, mean root diameter). Bars with the same letter are not significantly different according to Fisher LSD test (P < 0.05).

Results

Grasshopper density affected most of the aboveand below-ground variables of early stage growth of both small-grains and canola (Table 1). Regardless of crop type, damage caused by grasshopper feeding was more pronounced on the above- than below-ground plant parts, probably because below-ground plant parts were affected only indirectly by grasshopper feeding (Table 2; Figs. 2 and 3). These variables also differed among crops (Table 1). Under all grasshopper densities, small grains, barley and oats in particular, had a much higher above- and below-ground plant growth and carbon to nitrogen ratio than canola (Figs. 2 and 3 and 4).

Grasshopper Damage Influences on Leaves and Stems. Grasshopper damage to both leaf and stem ranged from slight, in the low-density barley and oats treatments, to total destruction in the high-density canola and wheat treatments. Leaf area and mass declined with increasing grasshopper numbers more sharply for wheat and canola than for barley and oats. For example, the reduction in leaf area of barley and oats, compared with the control, was $\approx 55\%$ under the high grasshopper density, whereas wheat and canola were completely consumed (100% reduction) at high grasshopper numbers (Table 2 and Fig. 2a). Although the relative reduction in leaf biomass was greatest on canola, reduction in leaf mass was greater, in absolute terms, for the small grains. For example, the difference in leaf weight between control and moderate grasshopper density was 0.27 g for barley and 0.16 g for canola.

Because grasshoppers prefer more digestible and nutritious leaves, as long as sufficient leaf tissue remained (as in oats and barley), stems were unaffected by grasshopper feeding, especially at low and medium grasshopper densities (Fig. 2). Stem growth in barley and oats was not affected except at the highest grasshopper density. In wheat and canola, stem weights were affected at lower grasshopper numbers than in barley and oats (Fig. 2). Reduction in stem biomass was a result of the combined effects of direct feeding damage as well as reduced stem growth.

Grasshopper Damage Influences on Root Growth and Morphology. As grasshopper density increased, growth of roots decreased (Fig. 3), but to a lesser degree than the above-ground plant biomass (Table 2). All root measurements, with the exception of average diameter, were significantly affected by grasshoppers in all crops (Table 1). Root length, pooled over all grasshopper densities was significantly different among crops with barley having the highest mean values followed by oats then wheat and canola (Fig. 3b). At the highest grasshopper density, root lengths in barley and oats were reduced by 26 and 28%, respectively, compared with 54 and 90% for wheat and canola, respectively (Table 2). In our study, based on measured variables, small grains tended to have a more vigorous root structure than canola and this was also reflected on their greater above-ground plant biomass than canola. Grasshopper feeding did not affect average root diameter, although root diameter differed among crops (Fig. 3c). Average root diameter pooled across grasshopper density was higher for barley and oats than wheat and canola (Fig. 3c).

Grasshopper Damage in Relation to C:N Ratio of Leaves and Stems. The carbon to nitrogen ratio in leaves differed only between the control and the highest grasshopper density for group 1 crops (barley and oats, Fig. 4). The carbon to nitrogen ratio of stems differed among grasshopper densities only for barley (Fig. 4). No effects of grasshopper feeding on C:N ratios were detected for wheat and canola (Fig. 4). However, the carbon to nitrogen ratio differed among crops (Fig. 4) (with canola having the lowest ratio). The C:N ratio value of crops pooled over all grasshopper densities ranged from 6.5 to 9.3 and 8.7–14.6 for leaves and stems, respectively (Fig. 4a and b).

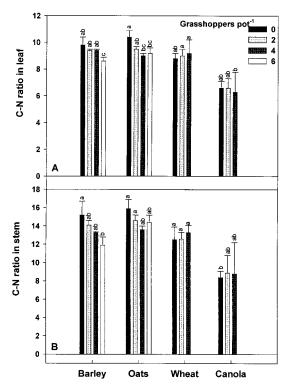


Fig. 4. Effects of grasshopper feeding on carbon to nitrogen ratio of plant tissues from seedlings of four crops. (A, leaves; B, stems). Comparisons of treatments were within crop groups (group 1: barley and oats; group 2: wheat and canola). Bars with the same letter are not significantly different according to Fisher LSD test (P < 0.05).

Discussion

Reduction in leaf area by herbivorous insects may be a result of a combined effect of direct consumption of leaf tissues, reduced growth of new leaf tissue, and expansion of holes in the leaf as the leaf expands (Hunt et al. 1995). Growth of new leaf tissue may be impaired by the lesser amount of photosynthetically active tissue, by reduced rates of photosynthesis in tissues surrounding the damage (Zangerl et al. 2002), or by the cost of defense-related chemical synthesis (Niemeyer 1988, Zangerl et al. 2002). It was impossible to determine how much each factor contributed to the reduced leaf area in this experiment, but the amount attributable to reduced growth may be comparable to that for roots, which were not directly damaged. The reduction in leaf area for barley and oats was ≈55%, whereas wheat and canola had a 100% reduction in leaf area under high-grasshopper density (Table 2 and Fig. 2a). In other crops, such as soybean, defoliation up to 33% has been shown to be tolerated with little impact on yield, although this depends on interactions with other environmental factors (such as soil moisture and soil fertility) (Pedigo et al. 1986, Haile et al. 1998) and timing of defoliation. Delayed senescence is the most widely and commonly reported plant response to defoliation. Under longer growing seasons, yield reductions may be minimal with delayed senescence; plants may experience improved light, water, and nutrient status after defoliation, compared with undefoliated plants (Higley 1992, Haile et al. 1998), which could compensate for the reduced leaf area. Under short growing seasons, such as in Alaska, plants may not have enough time to compensate for insect injury.

Our data show that all levels of grasshopper damage reduced root growth in all crops. The lack of any differences in mean root diameter indicates that the proportion of fine roots was not affected by grasshopper feeding. Because the plants were harvested to measure leaf, stem and measure root morphology we did not determine the effect of the early-season grasshopper damage on final yield of the plants. Yet, final yield of any crop depends on the initial development and growth of seedlings, especially under short growing seasons. Crops with well established root systems may be better able to use localized supplies of available soil water and nutrients, and successfully compete with weeds. Recovery or regrowth of plants occurs only if the growing points are undamaged. Therefore, small-grains with bigger root systems and better tolerance to grasshopper feeding may recover from defoliation more readily than canola. The smallgrain crops had a significantly greater above- and below-ground plant parts than canola. The large amount of nutrients stored in the seeds and faster germination of small-grains allow rapid establishment of vigorous root systems that might enable these crops obtain nutrients at a faster rate and recover rapidly and, therefore, tolerate a higher degree of grasshopper feeding, as opposed to crops, such as canola, with smaller seeds and correspondingly slower development of root systems. Moreover, with rapid growth small grains such as barley and oats attain more mass and have more buffer tissue to lose than canola.

We observed little or no differences in C:N ratios among levels of grasshopper density in leaf and stem tissues because of grasshopper feeding, except for higher C:N ratios in leaves of barley and oats, and also stems of barley, between the highest levels of grasshoppers and the controls. Alterations in C:N ratios of different tissues may be more likely with phloemfeeding insects, which assimilate carbohydrates and amino acids directly from the phloem stream (Byrne and Miller 1990, Palumbo et al. 2000, Watanabe and Kitagawa, 2000).

The amount of leaf tissue consumed by a given density of grasshoppers depends on many interacting factors: the insect's feeding rate (influenced by temperature, size of the insect and its physiological state) (Holmberg and Hardman 1984, Pfadt 1994, Lactin and Johnson 1995, Milbrath et al. 1998); the presence or absence of alternative food sources (such as weeds) that the insect may prefer (Harris et al. 1984); and the relative palatability and suitability of the host plant as food for the insect (Hinks and Olfert 1992, Milbrath et al. 1998). Of particular relevance to this experiment are observations of compensatory feeding by grasshoppers, i.e., consumption of greater quantities of lower quality food to obtain adequate nutrients

(McGinnis and Kasting 1967, Yang and Joern 1994). Although grasshoppers in this experiment consumed a greater proportion of leaf biomass of canola than the small grains, the absolute amount of canola consumed was much less (Fig. 2) than the small grains. This difference may be because of the apparently higher concentrations of nitrogen in the canola leaves (Fig. 4). Rates of consumption by grasshoppers may also differ between cultivars of a single crop (Hewitt 1969, Olfert et al. 1988, Hinks and Olfert 1992, Hinks et al. 1992). Because only one cultivar of each crop was employed in this experiment (those of most importance in the region of interior Alaska), results may differ somewhat if other cultivars were used.

Conclusions. Generally, both the above- and belowground growth and morphology of barley, oat, wheat, and canola were significantly affected by grasshopper feeding. However, reductions in growth from grasshopper feeding were somewhat more pronounced in above- (leaf area and leaf dry weight) than in belowground plant parts (root dry weight and root length). There was little or no effect of grasshopper feeding on stem dry weight of barley and oat, average root diameter, or carbon to nitrogen ratio of both leaf and stem tissue of all crops. Wheat and canola were found to be more susceptible to grasshopper feeding than were barley and oats for both above- and belowground parts. Although the degree of reduction in both above- and below-ground growth among grasshopper density levels and crops varied, grasshopper density ≥2 pot⁻¹ which is approximately equivalent to 50 hoppers m⁻² of first-instar grasshoppers could be very damaging to small-grain and oilseed crops, especially in a region like Alaska where the growing season is very short and time is critical for seedling establishment and growth.

Acknowledgments

We thank Linda DeFoliart, Beth Goggans, Andrew Cyr, and Amal Ajmi for technical assistance. Heather McIntyre and Tracy Williams facilitated access to the environmental chambers. Chris Viets provided grasshopper eggs and Charles Knight and Bob Van Veldhuizen generously donated seeds. We also thank Linda De Foliant, Steve Sparrow and Robert Van Veldhuizen for reviewing the earlier version of the manuscript. We are grateful to all anonymous reviewers, and L. Higley for comments on the earlier version of the paper.

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Received for publication 21 August 2002; accepted 24 April 2003.